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PHOSPHORUS CONTENTS IN DESERT RIPARIAN SPIDERS AND INSECTS VARY AMONG TAXA AND BETWEEN FLIGHT CAPABILITIES

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Abstract

Phosphorus occurs in a variety of biological molecules including DNA and RNA, ATP and other adenine nucleotides, phosphorylated metabolites, and phospholipids. Variation in phosphorus content among spiders and insects would influence the element's uptake by insectivorous birds. I measured amounts of phosphorus in 3 families of spiders and 7 orders and 24 families of insects collected in riparian habitat next to the Colorado River in western Arizona. Relation between phosphorus mass and body dry-mass, $P\,\mu g = 9.6\,(body\ mg)$, in spiders and insects was not allometric. Phosphorus concentration, as a mean percentage of body dry-mass, was higher in spiders (1.33%) than in insects (0.96%). Phosphorus contents varied most among families but also among orders and genera. Insect predators contained higher phosphorus concentrations (1.01%) than insect herbivores (0.90%). Strong-flying insects, Odonata, Neuroptera, Diptera, and Hymenoptera except Formicidae, also contained higher phosphorus concentrations (1.04%) than weak flying or wingless insects (0.89%), Orthoptera, Hemiptera, Coleoptera, and Formicidae. Larger flight-muscles with higher concentrations of phosphorylated metabolites likely increase phosphorus contents in strong-flying insects. Birds that eat aerial insects may benefit from higher phosphorus contents in their prey.

Key Words: Araneae, Insecta, nutrients, predators, flight muscles, insectivorous birds

Resumen

El fósforo occure en una variedad de moléculas biológicas, incluyendo ADN, ARN, ATP y otros nucleótidos de adenina, metabolitos fosforilados y fosfolípidos. La variación en el contenido de fósforo entre las arañas y los insectos pueden influir en el forrajeo de las aves insectívoras. Se midió la cantidad de fósforo en 3 familias de arañas y 24 familias pertenecientes a 7 órdenes de insectos recolectados en el hábitat ribereño junto al río Colorado en el oeste de Arizona. La relación entre la masa de fósforo y la masa corporal en seco, $P\,\mu g =$ 9.6 (mg cuerpo), en las arañas y los insectos no fue alométrica. La concentración de fósforo, como un porcentaje medio de masa corporal en seco, fue mayor en las arañas (1.33%) que en los insectos (0.96%). El contenido de fósforo varió más entre las familias, pero también entre los órdenes y géneros. Los insectos depredadores tenian una mayor concentración de fósforo (1.01%) que en los insectos herbívoros (0.90%). Los insectos que son voladores fuertes, Odonata, Neuroptera, Diptera, y Hymenoptera menos la familia Formicidae, también tenian una alta concentración de fósforo (1.04%) que en insectos que son voladores débiles o sin alas (0.89%), Orthoptera, Hemiptera, Coleoptera y Formicidae. Los músculos de vuelo mas grandes con mayores concentraciones de metabolitos fosforilados probablemente aumentan el contenido de fósforo en los insectos que son voladores fuertes. Las aves que se alimentan de insectos aéreos pueden beneficiarse del contenido mayor de fósforo en sus presas.

Palabras Clave: Araneae, Insecta, nutrientes, depredadores, músculos de vuelo, aves insectívoras

Biological molecules containing phosphorus (P) are involved in a variety of functions including protein synthesis and energy production and storage. Phosphorus bonds with oxygen to form phosphate (PO_4^{3-}), a molecular ion that can string together or bond to other compounds. Phosphates bonded to nucleosides, compounds comprised of a sugar attached to a purine or pyrimidine base, form nucleotides that can polymerize into the DNA and RNAs involved in protein synthesis. One or more phosphates attached to the nucleoside adenosine form the adenine nucleotides AMP, ADP, and ATP involved in energy storage. Phosphates from ATP temporarily bond to intermediate compounds during metabolism of glucose by glycolysis, enabling energy production. Phosphates also occur in phospholipids, molecules

with polar and non-polar ends that form layers necessary for membrane structure.

Variation in P concentration among spiders and insects has been little studied. Woods et al. (2004) measured P contents in spiders (Araneae) and 7 orders of insects collected in the Sonoran Desert. They found that P concentrations (averaging 0.79% of body dry-mass) allometrically decreased with body mass, were higher in Araneae, Lepidoptera, and Diptera after adjusting for allometry, and were similar between insect herbivores and predators.

Phosphorus in insects has been implicated as an essential nutrient for birds. The red grouse (*Lagopus lagopus scotica* [Latham]; Galliformes: Phasianidae) is a plant-feeding bird that supplements its diet with insects, especially the crane flies *Tipula* and *Molophilus* (Diptera: Tipulidae) (Butterfield & Coulson 1975). Butterfield & Coulson estimated that P accounts for 0.90% of body dry-mass in *Tipula* and 0.26% in *Molophilus* and suggested that crane flies are an important source of P for red grouse. Skylarks (*Alauda arvensis* L.; Passeriformes: Alaudidae) also have been hypothesized to increase P intake by augmenting their plant diet with insects, mostly beetles (Green 1980).

Concentrations of nitrogen (N) and sulfur (S), other nutrients essential to birds, were previously measured in spiders and insects collected in desert riparian habitat created for wildlife (Wiesenborn 2011, 2012). This study measured P concentrations in spiders and insects collected at the same locality. The following questions were examined: (1) Does P mass allometrically increase with body mass? (2) What are the relative contributions of class, order, family, and genus to variation in P concentration? (3) Does P content vary among trophic levels in insects? (4) Is P concentration related to flight capability in insects?

Materials and Methods

Collecting and Identifying Spiders and Insects

Spiders and insects were collected next to the Colorado River within Havasu National Wildlife Refuge in Mohave County, Arizona. Most arthropods were collected at an irrigated 43-ha riparian restoration area (N 34° 46' W 114° 31'; 143 m asl) of planted or volunteer trees and shrubs 12 km southeast and across the river from Needles, California. Plots were planted during 2003-2005 with cuttings that were taken from nearby areas along the river. The area lies between Topock Marsh (16 km^2) and Beal Lake (0.9 km^2), 2 impoundments containing mostly emergent cattails (*Typha* sp.; Typhales: Typhaceae) and open water. Undeveloped areas of the surrounding floodplain support mostly naturalized tamarisk shrubs (*Tamarix ramosissima* Ledeb.; Caryophyllales: Tamaricaceae). The floodplain is flanked by Sonoran desertscrub dominated by creosote bush (*Larrea tridentata* [DC.] Cov.; Zygophyllales: Zygophyllaceae). Maximum air temperatures at Needles average 42.7 °C during Jul and 17.7 °C during Dec (DRI 2012).

I collected arthropods from plants and trapped insects in flight. Arthropods were swept with a 38-cm diam muslin net from planted cottonwood (*Populus fremontii* S. Watson; Malpighiales: Salicaceae) and Goodding's black willow (*Salix gooddingii* C. Ball; Malpighiales: Salicaceae) trees, volunteer honey mesquite (*Prosopis glandulosa* Torrey; Fabales: Fabaceae) and screwbean mesquite (*Prosopis pubescens* Benth.) trees, and volunteer arrowweed shrubs (*Pluchea sericea* [Nutt.] Cov.; Asterales: Asteraceae). I also swept arthropods from *T. ramosissima* bordering the plots and narrow-leaved willow shrubs (*Salix exigua* Nutt.; Malpighiales: Salicaceae) along a dirt canal 2 km northwest of the plots. Plant species were swept separately except for *Prosopis* spp., which grew together. Each species was swept 10-15 min on 9 dates: 30 Apr, 16 & 29 May, 12 & 25 Jun, 9 & 23 Jul, and 6 & 20 Aug 2012. All plant species flowered and fruited except for *P. fremontii*. Arthropods swept from plants were placed into plastic bags and killed under direct sunlight. Flying insects were captured with a Townes-style Malaise trap (MegaView Science, Taichung, Taiwan) that was elevated 1-m aboveground within a plot of *S. gooddingii* and *P. sericea*. Trapped insects were collected into 70% ethanol. Insects were trapped for 45-90 min during 0930-1200 MST on the same 9 dates.

Spiders and insects in each sweeping were sorted under a microscope into groups of similar-looking specimens. Representatives of each group were placed into 70% ethanol for identification. I counted and split the remaining specimens of each arthropod group into samples with an estimated dry mass > 2 mg. Arthropod samples for P analysis were cleaned with a small brush and stored in open shell vials.

Spiders and adult insects except Chrysopidae were identified at least to genus. I assumed nymphal Acrididae to be the same species as adult *Melanoplus herbaceus* Bruner swept from the same *P. sericea* plants, the grasshopper's primary host (Strohecker et al. 1968). Pentatomid nymphs were matched against *Brochymena sulcata* Van Duzee adults. Mantidae nymphs were identified to family. Insects were identified as nymphs or adults, whereas spiders were not differentiated as juveniles or adults. Vouchers of insects identified to genus except for honeybees, *Apis mellifera* L., were deposited at the Entomology Research Museum, University of California, Riverside. Vouchers of spiders were deposited at the California Academy of Sciences, San Francisco.

Measuring Phosphorus Contents

Arthropod samples analyzed for P content were dried, weighed, and digested. They were dried 4 h at 95 °C and weighed (± 1 µg) with a microbalance (C30, Cahn Instruments, Cerritos, California). Dried samples > 2 mg were individually digested in a 23-mL microwave acid-digestion vessel (no. 4781, Parr Instrument, Moline, Illinois). I transferred arthropods into the vessel's inner cup and added 2.5 mL of trace-metal grade nitric acid. Samples with dry mass > 40 mg received 3.0 mL of nitric acid. The vessel was placed into a 700 W microwave oven at full power for 20 sec. After cooling for 30 min, the resulting clear liquid was rinsed from the cup and its cap with water into a beaker. I brought the rinse to 50 mL, or to 60 mL if 3.0 mL of nitric acid was used, with a volumetric flask. Different masses (0.397, 1.356, 2.350, 3.715, 8.760 mg) of adenosine 5'-monophosphate (8.92% P, Acros Organics, Fair Lawn, New Jersey), weighed with the microbalance, and a blank were similarly digested to produce a range of P concentrations (0.708-15.6 µg/ml) for use as standards.

Phosphorus concentrations in digested samples of arthropods were measured against the standards with an Inductively-Coupled Plasma Atomic Emission Spectrometer (Optima 7300 DV, Perkin Elmer, Waltham, Massachusetts) that detected ultraviolet emission from P at 213.617 nm. Light was detected during an automatic read-time (1-5 sec) for each sample and its intensity quantified as the area under the peak. Operating conditions of the spectrometer included a radio frequency power of 1.45 kW, an outer argon flow of 15 L/min, a nebulizer argon flow of 0.6 L/min, and a viewing height of 15.0 mm. Arthropods were analyzed in 9 batches, 1 for each collecting date, of 12-30 samples using the same standards. Linear correlation coefficients between light intensity and calculated P-concentration in the standards were > 0.99.

Phosphorus concentration, [P], in each arthropod sample was adjusted for variation among batches by using concentrations in an undigested, phosphate Standard Reference Material (SRM), containing 2.61 µg P/mL (ERA, Arvada, Colorado), measured across batches:

[P]sample, adjusted = [P]sample X [P]SRM, mean across batches/[P]SRM in batch

Phosphorus concentration in the undigested SRM was inflated to an average 3.75 (range 3.59-3.86) µg/mL across batches, indicating that an average 69.6% of P was recovered from the digested AMP standards. Recoveries of P in the arthropod samples were assumed to be the same as in the standards. Adjusted P-concentration was multiplied by final rinse-volume (mL) to calculate P mass (µg). I also calculated %P of arthropod dry-mass in each sample.

Relating Phosphorus Mass to Body Mass

I examined if P mass in spiders and insects was allometrically (exponentially) related to body dry-mass. Arthropod mass and P mass were divided by the number of specimens in each sample. Allometry was determined by regressing log (*P µg*) against log (*body mg*) and testing if the regression coefficient $b_1 \neq 1$ (the exponent of *body mg* in the back-transformed, allometric equation) with a 2-tailed approximate *t* test (Neter et al. 1996). For plotting, P mass and body dry-mass were averaged within genera.

Comparing Phosphorus Contents Among Taxa

Phosphorus contents of arthropod samples were compared between classes and among orders, families, and genera. I transformed P concentrations with $2[\arcsin(\%P/100)^{1/2}]$. Transformed %P was compared between spiders and insects with an analysis of variance. I repeated the analysis and determined if classifying arthropods by order instead of class, by family instead of order, and by genus instead of family, explained more variation in transformed %P with the general linear test approach (Neter et al. 1996). This approach tests if the mean square error in an analysis of variance decreases significantly when the model becomes more complete (with more model df).

Comparing Phosphorus Contents Among Trophic Levels and Between Flight Capabilities

Phosphorus contents of insects were compared among trophic levels. Insects were classified as herbivore, predator, or detritivore with descriptions of primary diet. Descriptions included Cole (1969) for Diptera, Essig (1926) for Tettigoniidae, Pentatomidae, and Formicidae, and Borror et al. (1981) for the remaining taxa. Holometabolous insects were classified by larval diet. Herbivores included consumers of pollen, nectar, or homopteran egesta, and predators included parasites. Transformed %P was compared among trophic levels with an analysis of variance. I also compared herbivores with predators, and detritivores with herbivores and predators combined, with contrasts.

Phosphorus contents were compared between insects categorized as strong fliers and those categorized as weak fliers or wingless. Strong-flying insects included Odonata, those with indirect flight muscles (Diptera and Hymenoptera except Formicidae), and Chrysopidae due to their flight behavior to lights. All other insects were categorized as weak flying or wingless. I compared transformed %P between the 2 categories with an analysis of variance. Comparisons among taxa and trophic levels and between flight capabilities are not independent of each other, because insect taxon, trophic level, and flight capability are all confounded.

Results

I collected 14 samples of 16 spiders species representing 3 families and 4 genera (Table 1). Most spiders collected were the crab spiders *Mecaphesa*, primarily *Mecaphesa celer* (Hentz) (Araneae: Thomisidae) or closely related, and the jumping spiders *Habronattus* (Araneae: Salticidae), primarily *Habronattus hirsutus* (Peckhams). Spiders were found on 5 of the 6 plant-species. I collected 132 samples of 467 insects representing 7 orders, 24 families, and 25 identified genera (Table 1). The most abundant insects collected were the weevils *Coniatus splendidulus* F. that were recently introduced onto *T. ramosissima* in the U.S. (Eckberg & Foster 2011). All insects collected were adults except for nymph and adult *M. herbaceous* grasshoppers and *B. sulcata* stink bugs and nymph mantids (Mantidae). Mean body dry-mass of spiders and insects (Fig. 1) ranged from 0.28 mg in the dolichopodid fly *Asyndetus* to 79.5 mg in the katydid *Insara elegans* (Scudder).

Trophic levels of insects (Table 1) included 68 samples of herbivores in 12 families and 14 genera, 56 samples of predators in 11 families and 10 identified genera, and 8 samples of detritivores representing a single species. The most-collected herbivores were the generalist ant *Formica xerophila* M. R. Smith, *C. splendidulus* weevils, and the chrysomelid beetle *Algarobius prosopis* LeConte that feeds on mesquite seeds (Kingsolver 1972). The most-collected predators were the deer fly *Tabanus subsimilis* Bellardi, caught in the Malaise trap, and the tiphiid wasp *Myzinum frontalis* (Cresson), presumed parasites of scarab larvae (Kimsey 2009) that occurred in large swarms of males around *P. sericea*. All detritivores were the lauxaniid fly *Minettia flaveola* Coquillett, consumers of rotting leaves (McDonald et al. 1974).

Strong-flying insects included 65 samples in 4 orders and 12 families, and weak-flying or wingless insects included 67 samples in 4 orders and 12 families (Table 1). Most strong-flying insects were predators (42 samples), with *T. subsimilis* and *M. frontalis* comprising the largest number of samples. Most weak-flying or wingless insects were herbivores (53 samples), with *F. xerophylla* and *C. splendidulus* comprising the largest number of samples.

Relation of Phosphorus Mass to Body Dry-Mass

Phosphorus mass in spiders and insects increased linearly with body dry-mass (Fig. 1). Phosphorus mass and body dry-mass were related (t = 53.3; df = 132; $P < 0.001$) by log (P µg) = 0.983 + 1.005[log (*body mg*)]. Body dry-mass explained 95% of variation in P mass. The b_1 coefficient of 1.005 did not differ from 1 (t = 0.26; df = 144; P = 0.79), signifying that the relation between P mass and body mass was not allometric. Setting b_1 = 1 and back-transforming the regression equation produced $P\ \mu g = 9.6(body\ mg)$.

Phosphorus Contents Among Taxa

Arthropod taxa varied in P content (Table 1). Phosphorus concentrations differed between spiders and insects (F = 17.7; df = 1, 144; $P < 0.001$), and these 2 taxa, representing different classes, explained 11% of variation in transformed %P. Mean P concentrations, as percentages of dry mass, were 1.33% in spiders and 0.96% in insects. Classifying arthropods by order instead of class explained a significant (F = 10.9; df = 6, 138; $P <$ 0.001) proportion of additional variation (29%) in P content. Within insects, mean P concentrations differed most between Coleoptera (0.66%) and the other 6 orders (1.00%). A significant (F = 8.00; df = 19, 119; $P < 0.001$) proportion of additional variation (34%) in P concentration was explained when arthropods were classified by family instead of order. This additional variation was partly due to lower mean P concentrations in Pentatomidae (0.76%) compared with other Hemiptera (0.96%), in the single species (*Acinia picturata* Snow) of Tephritidae (0.79%) compared with other Diptera (1.23%), and in Tiphiidae (0.69%) and Vespidae (0.76%) compared with other Hymenoptera (1.10%). Classifying arthropods by genus instead of family also explained a significant (F = 2.95; df = 9, 110; P = 0.004) proportion of additional variation (4.8%) in P content. Mean P concentrations in the reduviids *Phymata* (0.70%) and *Zelus* (1.10%), the membracids *Stictopelta* (0.66%) and *Tylocentrus* (0.99%), and the cicadellids *Acusana* (1.11%) and *Homalodisca* (1.57%) contributed most of the variation among genera. Class, order, family, and genus described 79% of variation in %P.

Phosphorus Contents Among Trophic Levels and Between Flight Capabilities

Insect herbivores, predators, and detritivores contained different P concentrations (Fig. 2). Transformed %P varied among trophic levels (F = 3.47; df = 2, 129; P = 0.034). Phosphorus contents (back-transformed mean, ± SE) were higher (t = 2.27; df = 129; P = 0.025) in predators (1.01, 0.98-1.06%) than in herbivores (0.90, 0.87-0.93%). Concentrations of P in herbivores and predators combined (0.96, 0.93–0.98%) did not differ (t = 1.29; df = 129; P = 0.20) from those in detritivores (1.10, 1.01–1.19%). Trophic level explained 5.1% of variation in transformed %P.

Strong flying insects and weak flying or wingless insects also contained different P concentrations (Fig. 2). Transformed %P differed between the 2 flight capabilities (F = 8.39; df = 1, 130; P = 0.004). Phosphorus contents (back-transformed mean, ± SE) were higher in strong-flying insects

TABLE 1. SPIDERS AND INSECTS COLLECTED IN RIPARIAN HABITAT NEAR THE COLORADO RIVER IN ARIZONA AND ANALYZED FOR PHOSPHORUS CONTENT.

Order[1]	Family	Genus	Source[2]	No. samples	No. specimens per sample	Trophic level[3]	Flight capability[4]	Mean body dry mass (mg)	Mean ± SD %P
Araneae	Philodromidae	*Philodromus*	F,G	2	1–2	P	—	1.8	1.46 ± 0.03
	Thomisidae	*Mecaphesa*	E,G,P,S	6	1–2	P	—	4.2	1.31 ± 0.18
	Salticidae	*Habronattus*	E,S	5	1	P	—	3.9	1.35 ± 0.20
		Sassacus	F	1	1	P	—	2.1	1.15
Odonata	Libellulidae	*Pachydiplax*	F,T	7	1	P	S	51.4	1.03 ± 0.08
Orthoptera	Acrididae[5]	*Melanoplus*	S	8	1–3	H	W	26.9	1.09 ± 0.13
	Tettigoniidae	*Insara*	S	1	1	H	W	79.5	0.89
	Mantidae[6]	—	E,F,S,T	4	1	P	W	25.8	1.10 ± 0.19
Hemiptera	Pentatomidae[5]	*Brochymena*	P,S	3	1	P	W	39.2	0.78 ± 0.29
	Reduviidae	*Phymata*	E,S	2	1–2	P	W	7.3	0.70 ± 0.02
		Zelus	E,F,S	3	1	P	W	8.5	1.11 ± 0.16
	Membracidae	*Stictopelta*	P	5	1	H	W	15.5	0.66 ± 0.05
		Tylocentrus	P	1	2	H	W	2.6	0.99
	Cicadellidae	*Acusana*	E,G	3	1–2	H	W	3.9	1.12 ± 0.13
		Homalodisca	E,S	2	1	H	W	7.6	1.57 ± 0.11
	Cixiidae	*Oecleus*	G	2	2–6	H	W	1.4	1.07 ± 0.11
Neuroptera	Chrysopidae	—	F,S	3	3	P	S	2.4	1.13 ± 0.17
Coleoptera	Coccinellidae	*Chilocorus*	F	1	2	P	W	4.3	0.86
	Chrysomelidae	*Algarobius*	E,F,P,S	9	1–6	H	W	3.0	0.74 ± 0.09
	Curculionidae	*Coniatus*	T	11	4-26	H	W	0.93	0.57 ± 0.05
Diptera	Tabanidae	*Tabanus*	F,G,M	14	1	P	S	15.4	1.39 ± 0.26
	Dolichopodidae	*Asyndetus*	M	3	7–18	P	S	0.28	1.37 ± 0.43
	Tephritidae	*Acinia*	F,G	6	2–6	H	S	1.2	0.80 ± 0.12
	Lauxaniidae	*Minettia*	F,G,P,S	8	1–6	D	S	2.9	1.11 ± 0.25
	Tachinidae	*Zaira*	M	4	1–2	P	S	5.5	0.90 ± 0.09

[1]Araneae are juveniles and adults; other orders are adults unless noted.
[2]E, *Salix exigua*; F, *Populus fremontii*; G, *Salix gooddingii*; M, Malaise trap; P, *Prosopis glandulosa* or *P. pubescens*; S, *Pluchea sericea*; T, *Tamarix ramosissima*.
[3]D, Detritivore; H, Herbivore; P, Predator.
[4]S, Strong flying; W, Weak flying or wingless.
[5]Nymphs and adults.
[6]Nymphs.

TABLE 1. (CONTINUED) SPIDERS AND INSECTS COLLECTED IN RIPARIAN HABITAT NEAR THE COLORADO RIVER IN ARIZONA AND ANALYZED FOR PHOSPHORUS CONTENT.

Order[1]	Family	Genus	Source[2]	No. samples	No. specimens per sample	Trophic level[3]	Flight capability[4]	Mean body dry mass (mg)	Mean ± SD %P
Hymenoptera	Formicidae	*Formica*	E,F,G,P,S	12	3–9	H	W	0.85	1.11 ± 0.17
	Tiphiidae	*Myzinum*	S	9	1–2	P	S	13.3	0.69 ± 0.09
	Vespidae	*Polistes*	M,P,T	3	1	P	S	32.5	0.76 ± 0.09
	Halictidae	*Dieunomia*	S	4	1–2	H	S	6.5	1.12 ± 0.06
	Andrenidae	*Perdita*	S	2	1–2	H	S	2.8	0.95 ± 0.24
	Apidae	*Apis*	E,S	2	1	H	S	21.7	1.20 ± 0.26

[1]Araneae are juveniles and adults; other orders are adults unless noted.
[2]E, *Salix exigua*; F, *Populus fremontii*; G, *Salix gooddingii*; M, Malaise trap; P, *Prosopis glandulosa* or *P. pubescens*; S, *Pluchea sericea*; T, *Tamarix ramosissima*.
[3]D, Detritivore; H, Herbivore; P, Predator.
[4]S, Strong flying; W, Weak flying or wingless.
[5]Nymphs and adults.
[6]Nymphs.

(1.04, 1.00-1.07%) than in weak-flying or wingless insects (0.89, 0.86-0.93%). Flight capability explained 6.1% of variation in %P, slightly more than that explained by trophic level.

DISCUSSION

A linear, rather than allometric, increase in P mass as body mass increased contradicts previous work. Negative allometry in P content, with %P decreasing as body dry-mass increased, was detected across the various spiders and insects analyzed by Woods et al. (2004). Two hypotheses have been presented to explain decreasing P content with increasing body mass. First, larger organisms grow more slowly and require less P-containing compounds such as RNA for protein synthesis (Elser et al. 1996; Gillooly et al. 2005). Second, scaling laws require arthropod cuticles to thicken and comprise greater proportions of body mass as body mass increases, and cuticles contain low amounts of P (Woods et al. 2004). The first hypothesis, generated from observations of planktonic invertebrates, may apply to immature spiders and insects undergoing development but not to non-developing adults (Woods et al. 2004). Different growth rates would not cause negative allometry in P content across the mostly-adult spiders and insects examined in the present study. In contrast, positive allometry in cuticle mass would be expected to cause negative allometry in P content in adult arthropods. Greater cuticle thickness in larger spiders and insects from the same locality was inferred from N contents that exponentially-increased as body mass increased (Wiesenborn 2011). Phospholipids are the only P-containing compounds in arthropod cuticle, and they occur in very low amounts (Richards 1978). The greater range of body dry-masses (0.1 mg-1 g) examined by Woods et al. (2004), compared to those considered here (0.28-80 mg), may have enabled their detection of negative allometry in P content.

Higher concentrations of P in spiders compared with insects resemble a similar difference in S concentrations (Wiesenborn 2012). Phosphorus contents differed less between the 2 classes than S contents; P contents were 1.4 times higher in spiders than in insects, whereas S contents were 2.2 times higher. Venom production by spiders may increase P concentrations as suggested for S (Wiesenborn 2012). The venom of some spiders contains phosphoric acid and AMP, ADP, and ATP (Kuhn-Nentwig et al. 2011). All 3 adenine nucleotides occur in tarantula venom, and high concentrations of ATP synergistically increase venom toxicity (Chan et al. 1975). All spiders produce venom except Uloboridae, and the paired venom glands can occupy a large proportion of the prosoma (Foelix 1996). High concentrations of P-containing compounds in venom

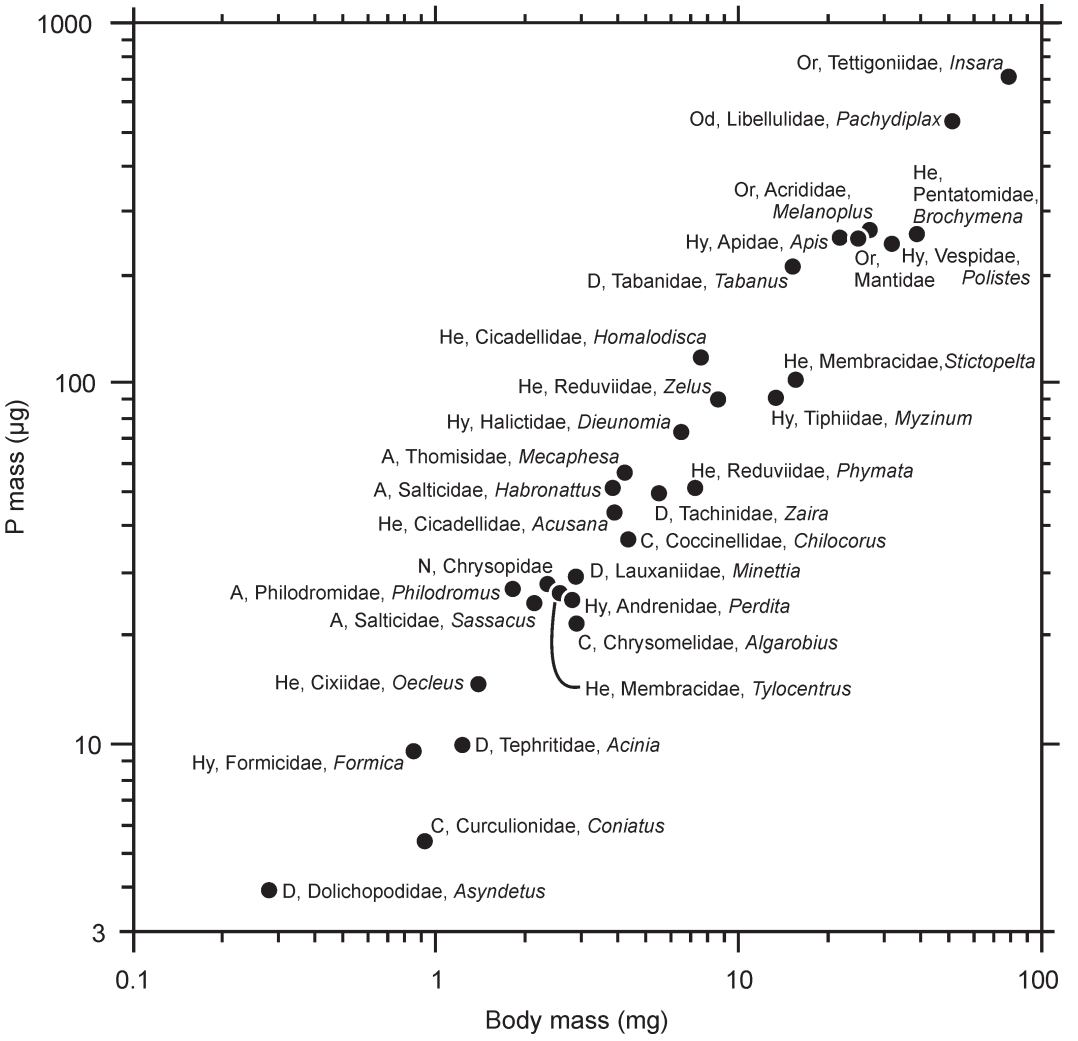

Fig. 1. Mean phosphorus mass vs. mean body dry-mass of spiders and insects collected from riparian plants near the Colorado River in Arizona. Axes are log scales. Orders shown as: A, Araneae; C, Coleoptera; D, Diptera; He, Hemiptera; Hy, Hymenoptera; N, Neuroptera; Od, Odonata; and Or, Orthoptera. All specimens are adults except Araneae are juveniles and adults, *Brochymena* and *Melanoplus* are nymphs and adults, and Mantidae are nymphs.

glands would elevate body P contents. Woods et al. (2004) also found relatively high P contents in spiders.

Low P content in Coleoptera corresponds with the order's low N and S contents (Wiesenborn 2011, 2012). Low concentrations of all 3 elements in Coleoptera may be due to chitin, a polysaccharide low in N and without S and P that combines with cuticular protein. High concentrations of cuticular chitin in beetles, especially in the elytra, may decrease body P concentrations. Phosphorus contents were more variable among arthropod families than were S and N contents. Families contributed 34% of variation in P content compared with 11% of variation in S content and 1.4% of variation in N content (Wiesenborn 2011, 2012). Lower P contents in Pentatomidae than in other Hemiptera may have been due to the coarsely hardened dorsal cuticle of *B. sulcata*, reflected in its common name of rough stink bug. A large contribution of cuticle dry-mass to body dry-mass would have lowered P content in *B. sulcata* similar to that hypothesized in beetles. Phosphorus contents also varied among genera, variation not detected in S (Wiesenborn 2012). Concentrations of P-containing compounds were more variable at lower taxonomic levels than the other elements examined.

Lower P contents in insect herbivores compared with insect predators contributed to the significant variation among families. The herbivorous tephritid, *A. picturata*, contained lower

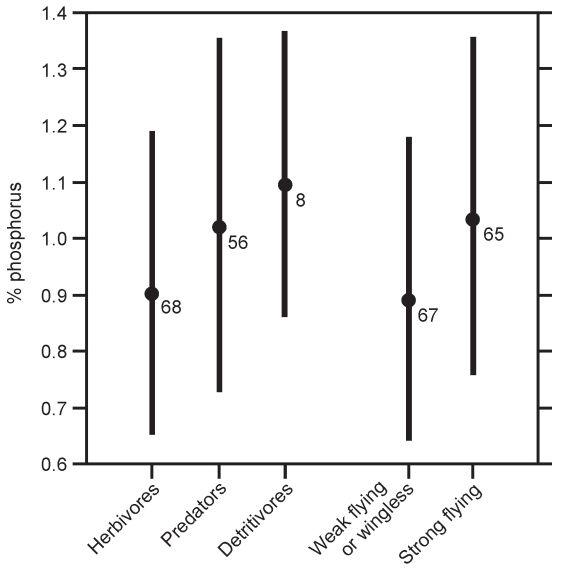

Fig. 2. Phosphorus contents as a percentage of body dry-mass in insects collected from riparian plants near the Colorado River in Arizona and categorized by trophic level and by flight capability. Points are means and vertical bars are ± SD's. Means and upper and lower bounds of SD's are back-transformed from percentages transformed $2[\arcsin(\%P/100)^{1/2}]$. Numbers next to means are sample sizes.

P contents than the other families of Diptera, all predators or detritivores. Larvae of *A. picturata* develop in *Pluchea* flowers (Foote et al. 1993) and reduce seed production (Alyokhin et al. 2001), suggesting consumption of ovaries or seeds. Concentrations of N in *A. picturata* were also relatively low (Wiesenborn 2011).

Concentration of elements upward through insect trophic levels, as detected here with higher P contents in predators than in herbivores, has been hypothesized but infrequently observed. Fagan et al. (2002) detected higher N concentrations in insect predators compared with herbivores after adjusting for allometry and phylogeny. They suggested that N contents in diets, being higher in plant-feeding insects than in plants, contribute to higher N concentrations in predators. I found N contents after accounting for allometry to be similar between herbivores and predators across arthropod orders, but lower in herbivores within Diptera due to *A. picturata* (Wiesenborn 2011). Sulfur contents also were similar between insect herbivores and predators (Wiesenborn 2012). Woods et al. (2004) did not detect different P contents between the 2 trophic levels in the desert insects they analyzed. Concentrations of P may not differ greatly between plant-feeding insects and the tissues they consume. Mean P content in the phytophagous insects analyzed here (0.90%) slightly exceeded that measured in leaves and stems (0.79% of dry mass), plant parts frequently eaten by insects, of various angiosperms (Broadley et al. 2004). The estimated increases in P concentration between plants and herbivores (0.11%) and herbivores and predators (0.10%) were similar.

Higher concentrations of P in predators may be more related to flight capability than diet. After the leafhopper *Homalodisca*, the predaceous flies *Tabanus* and *Asyndetus* contained the highest P concentrations and were the 2 genera most-frequently captured in flight by the Malaise trap. Strong-flying insects likely have greater flight musculature and higher energy demands. Phosphorus concentrations are especially high in insect flight muscle. Approximately half of the P in house flies, *Musca domestica* L. (Diptera: Muscidae), is found in flight muscle (Sacktor 1961). Of the 17 µg P measured in *M. domestica* flight muscle, 12 µg is contained in cytoplasm, and 5 µg is contained in mitochondria. Most P (85%) in cytoplasm occurs in phosphorylated metabolites, whereas most P (64%) in mitochondria occurs in phospholipids (Sacktor 1961). Phosphorylated metabolites in flight-muscle cytoplasm include the intermediate compounds produced during glycolysis. Flight muscles in flies also contain exceptionally-high concentrations of glycerol-3-phosphate (α-glycerophosphate, Sacktor 1961, Sacktor & Wormser-Shavit 1966), a metabolite that shuttles between cytoplasm and mitochondria. Nucleotides, mostly AMP, ADP, and ATP, make up 9% of P in *M. domestica* flight muscle and occur primarily in mitochondria (Sacktor 1961). Flight muscles likely comprise a large proportion of body mass in strong-flying insects and elevate percentages of body P.

Spiders and insects available to, and eaten by, insectivorous birds foraging in desert riparian habitat would contain different P contents. Aerial foraging by birds likely increases consumption of strong-flying insects that provide higher P concentrations. For example, the willow flycatcher (*Empidonax traillii* [Audubon]; Passeriformes: Tyrannidae) is a migratory bird that breeds in riparian habitat and captures aerial insects while flying and hovering (Sedgwick 2000). Diptera were the most-frequent insects eaten by willow flycatchers in southern Nevada and western Arizona, comprising 39% of prey and composed of a variety of families including Tabanidae and Dolichopodidae (Wiesenborn & Heydon 2007). Strong-flying Odonata, both dragonflies and damselflies, also were eaten by willow flycatchers with the former likely contributing a large proportion of diet biomass. Coleoptera, arthropods categorized as weak-fliers with the lowest P concentrations, comprised 9.5% of prey (Wiesenborn & Heydon 2007). Insectivorous birds like flycatchers that expend greater energy by capturing prey in flight

may benefit from the higher P concentrations that aerial insects provide.

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References Cited

Alyokhin, A. V., Messing, R. H., and Duan, J. J. 2001. Utilization of the exotic weed *Pluchea odorata* (Asteraceae) and related plants by the introduced biological control agent *Acinia picturata* (Diptera: Tephritidae) in Hawaii. Biocontrol Sci. Technol. 11: 703-710.

Borror, D. J., De Long, D. M., and Triplehorn, C. A. 1981. An Introduction to the Study of Insects, 5th ed. Saunders College Publishing, Philadelphia. xi + 827 pp.

Broadley, M. R., Bowen, H. C., Cotterill, H. L., Hammond, J. P., Meacham, M. C., Mead, A., and White, P. J. 2004. Phylogenetic variation in the shoot mineral concentration of angiosperms. J. Exp. Bot. 55: 321-336.

Butterfield, J., and Coulson, J. C. 1975. Insect food of adult red grouse *Lagopus lagopus scoticus* (Lath.). J. Anim. Ecol. 44: 601-608.

Chan, T. K., Geren, C. R., Howell, D. E., and Odell, G. V. 1975. Adenosine triphosphate in tarantula spider venoms and its synergistic effect with the venom toxin. Toxicon 13: 61-66.

COLE, F. R. 1969. The Flies of Western North America. Univ. California Press, Berkeley. xi + 693 pp.

Desert Research Institute (DRI). 2012. Western U.S. Climate Historical Summaries. Western Regional Climate Center, Reno, Nevada [http://www.wrcc.dri.edu/Climsum.html; accessed 30 Nov 2012].

Eckberg, J. R., and Foster, M. E. 2011. First account of the splendid tamarisk weevil, *Coniatus splendidulus* Fabricius, 1781 (Coleoptera: Curculionidae) in Nevada. Pan-Pac. Entomol. 87: 51-53.

Elser, J. J., Dobberfuhl, D. R., Mackay, N. A., and Schampel, J. H. 1996.Organism size, life history, and N:P stoichiometry: Toward a unified view of cellular and ecosystem processes. Bioscience 46: 674-684.

Essig, E. O. 1926. Insects of Western North America. The MacMillan Company, New York. xi + 1035 pp.

Fagan, W. F., Siemann, E., Mitter, C., Denno, R. F., Huberty, A. F., Woods, H. A., and Elser, J. J. 2002. Nitrogen in insects: Implications for trophic complexity and species diversification. American Nat. 160: 784-802.

Foelix, R. F. 1996. Biology of Spiders, 2nd ed. Oxford University Press, New York. 330 pp.

Foote, R. H., Blanc, F. L., and Norrbom, A. L. 1993. Handbook of the Fruit Flies (Diptera: Tephritidae) of America North of Mexico. Comstock, Ithaca, NY. 571 pp.

Gillooly, J. F., Allen, A. P., Brown, J. H., Elser, J. J., Del Rio, C. M., Savage, V. M., West, G. B., Woodruff, W. H., and Woods, H. A. 2005. The metabolic basis of whole-organism RNA and phosphorus content. Proc. Natl. Acad. Sci. U.S.A. 102: 11923-11927.

Green, R. E. 1980. Food selection by skylarks and grazing damage to sugar beet seedlings. J. Appl. Ecol. 17: 613-630.

Kimsey, L. S. 2009. Taxonomic purgatory: Sorting out the wasp genus *Myzinum* Latreille in North America (Hymenoptera, Tiphiidae, Myzinae). Zootaxa 2224: 30-50.

Kingsolver, J. M. 1972. Description of a new species of *Algarobius* Bridwell (Coleoptera: Bruchidae). Coleopt. Bull. 26: 116-120.

Kuhn-Nentwig, L., Stöcklin, R., and Nentwig, W. 2011. Venom composition and strategies in spiders: Is everything possible? Adv. In Insect Phys. 40: 1-86.

Mcdonald, J. F., Heed, W. B., and Miranda, M. 1974. The larval nutrition of *Minettia flaveola* and *Phaonia parviceps* and its significance to the Hawaiian leaf-breeding *Drosophila* (Diptera: Lauxaniidae, Muscidae, Drosophilidae). Pan-Pac. Entomol. 50: 78-82.

Neter, J., Kutner, M. H., Nachtsheim, C. J., and Wasserman, W. 1996. Applied Linear Statistical Models, 4th ed. McGraw-Hill, Boston. xv + 1408 pp.

Richards, A. G. 1978. The chemistry of insect cuticle, pp. 205-232 *In* M. Rockstein [ed.], Biochemistry of Insects. Academic Press, New York. xiv + 649 pp.

Sacktor, B. 1961. The role of mitochondria in respiratory metabolism of flight muscle. Annu. Rev. Entomol. 6: 103-130.

Sacktor, B., and Wormser-Shavit, E. 1966. Regulation of metabolism in working muscle *in Vivo*. J. Biol. Chem. 241: 624-631.

Sedgwick, J. A. 2000. Willow Flycatcher (*Empidonax traillii*), *In* A. Poole and F. Gill [eds.], The Birds of North America, no. 533. The Birds of North America, Inc., Philadelphia, PA. 32 pp.

Strohecker, H. F., Middlekauff, W. W., and Rentz, D. C. 1968. The Grasshoppers of California (Orthoptera: Acridoidea). Bull. California Insect Survey, vol. 10. Univ. California Press, Berkeley. v + 177 pp.

Wiesenborn, W. D. 2011. Nitrogen content in riparian arthropods is most dependent on allometry and order. Florida Entomol. 94: 71-80.

Wiesenborn, W. D. 2012. Sulfur contents of spiders and insects in desert riparian habitat. Florida Entomol. 95: 952-960.

Wiesenborn, W. D., and Heydon, S. L. 2007. Diets of breeding southwestern willow flycatchers in different habitats. Wilson J. Ornithol. 119: 547-557.

Woods, H. A., Fagan, W. F., Elser, J. J., and Harrison, J. F. 2004. Allometric and phylogenetic variation in insect phosphorus content. Funct. Ecol. 18: 103-109.